Acta Oecologica 52 (2013) 57–62

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Left–right asymmetries and shape analysis on *Ceroglossus chilensis* (Coleoptera: Carabidae)

Raffaella Bravi [a,1], Hugo A. Benítez [b,c,*]

[a] Environmental Biology Department, University Roma Tre, V. le G. Marconi 446, 00146 Rome, Italy
[b] Faculty of Life Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester M13 9PT, UK
[c] Instituto de Alta Investigación, Universidad de Tarapacá, Casilla 7-D, Arica, Chile

A R T I C L E I N F O

Article history:
Received 9 April 2013
Accepted 31 July 2013
Available online 29 August 2013

Keywords:
Ceroglossus
Geometric morphometrics
Fluctuating asymmetry
Directional asymmetry

A B S T R A C T

Bilateral symmetry is widespread in animal kingdom, however most animal can deviate from expected symmetry and manifest some kind of asymmetries. Fluctuating asymmetry is considered as a tool for valuating developmental instability, whereas directional asymmetry is inherited and could be used for evaluating evolutionary development. We use the method of geometric morphometrics to analyze left/right asymmetries in the whole body, in two sites and totally six populations of *Ceroglossus chilensis* with the aim to infer and explain morphological disparities between populations and sexes in this species. In all individuals analyzed we found both fluctuating asymmetry and directional asymmetry for size and shape variation components, and a high sexual dimorphism. Moreover a high morphological variability between the two sites emerged as well. Differences in diet could influence the expression of morphological variation and simultaneously affect body sides, and therefore contribute to the symmetric component of variation. Moreover differences emerged between two sites could be a consequence of isolation and fragmentation, rather than a response to local environmental differences between sampling sites.

1. Introduction

Most animals have a body plan that is symmetric, at least externally. Some morphological symmetries result from the repetition of parts in different positions or orientations (Klingenberg et al., 2002; Savriama and Klingenberg, 2011). In bilaterally symmetric organisms, bilateral symmetry can manifest itself in two ways: as object symmetry or matching symmetry (Mardia et al., 2000; Klingenberg et al., 2002). The first case happens whenever a structure is symmetric in itself and the plane of symmetry can divide the structure into two halves that are mirror images of each other. On the other hand matching symmetry happens every time a structure is present in one left and one right copy that can be matched, as they are mirror images of each other (Klingenberg et al., 2002; Savriama and Klingenberg, 2011).

It is very hard to find a real organism perfectly symmetric, and small asymmetries can reflect phenotypic adaptation to the environment. Floate and Fox (2000) and Piscart et al. (2005) suggested that the degrees of phenotypic disturbances reflect the ability of an individual to overcome the effects of stress; thus more symmetrical individuals would have greater survival possibilities than those with low levels of symmetry. On the other hand, environmental pressures and geographic distances affect microenvironments locally, and therefore their associated flora and fauna that are the result of adaptation over time to a specific environment (Alibert et al., 2001; Cepeda-Pizarro et al., 2003; Benítez et al., 2008). Organisms can deviate from the expected symmetric configuration and develop some kind of asymmetries, among which are fluctuating asymmetry (FA) and directional asymmetry (DA). The latter occurs whenever there is a greater development of a character on one side of the plane of symmetry than the other. Additionally, a proportion of DA has genetic bases (Van Valen, 1962; Palmer and Strobeck, 1986; Pelabon and Hansen, 2008; Carter et al., 2009) and its presence might be associated with the presence of developmental instability (Graham et al., 1993). Moreover FA is defined as the non-directional deviation from bilateral symmetry, also expressed as individual differences between left and right sides. Those deviations are normally distributed and have the mean of zero. Because of its characteristic, FA is generally considered suitable tool to infer developmental instability (Palmer and Strobeck, 1986).

* Corresponding author. Faculty of Life Sciences, University of Manchester, Michael Smith Building, Oxford Road, Manchester M13 9PT, UK. Tel.: +44 (0)161 306 7102; fax: +44 (0)161 275 5657.
E-mail address: hugo.benitez@postgrad.manchester.ac.uk (H.A. Benítez).
[1] Tel.: +39 0657338050; fax: +39 0657338052.

1146-609X/$ – see front matter
http://dx.doi.org/10.1016/j.actao.2013.07.007

Finally it is postulated that the degree of phenotypic symmetry is a mate-choice criterion, and as consequence anomalies in symmetry can be frequent enough to affect the evolution of sexual behavior; recurrence of asymmetrical sexual selected characters could happen if they are important under selection (West-Eberhard, 2005). The processes of sexual selection are believed to modify normally maintained symmetry in traits under stabilized selection, and consequently an increase in FA is expected (Møller and Pomiankowski, 1993; Tomkins and Simmons, 2003).

Ceroglossus chilensis (Eschscholtz, 1829) (Coleoptera: Carabidae) has 26 subspecies, distributed from the Maule Region and the extreme south of the Aysén Region (Chile); it is also present in Argentina, and is the southernmost species and the one with the widest distribution in Chile. This species prefers xeric habitats and it is more tolerant to arid conditions than its congeners. It is still matter of debate if its size, which is relatively large for a carabid, is related to its ability to resist the aridity of the environment (Jiroux, 2006). Some evidences indicate that the development and environmental instability of *C. chilensis*, which is a species with high activity density, can be affected by modified environmental conditions (Briones and Jerez, 2007; Benítez et al., 2008, 2011). Previous studies in *C. chilensis* have demonstrated that the similarities of males and females are directly associated with the sex ratio and very lowly with sexual dimorphism, the latter detectable only under a microscopy inspection (Benítez et al., 2010b, 2011).

In the present study we analyze left/right asymmetries with the method of geometric morphometric, in the whole body of several populations of *Ceroglossus chilensis*, to provide an explanation of the morphological disparities between populations and sexes in this species.

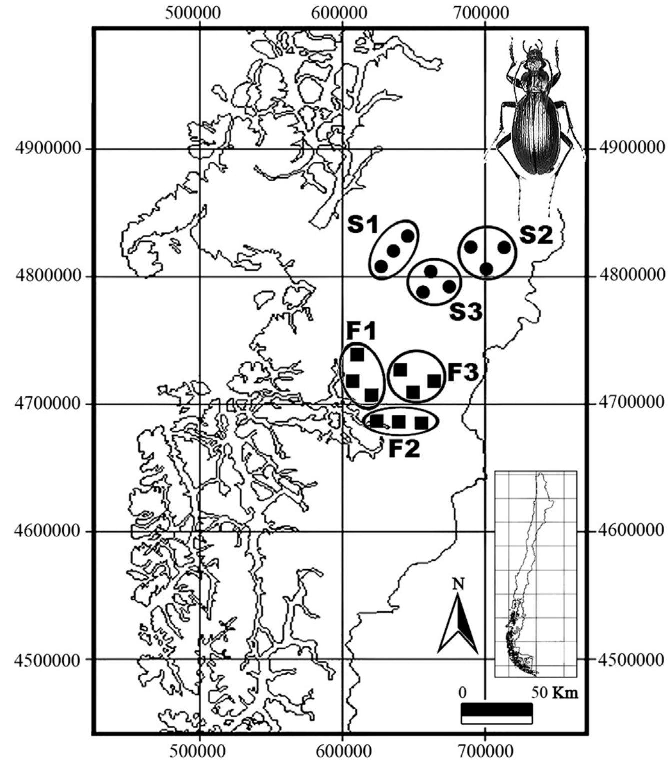

Fig. 1. Map of Chile and the Aysén Region, indicating the study area and the sampling sites. Circles: Second-Growth Stand, Squares: Forest.

2. Materials and methods

2.1. Data acquisition

Three populations in mature forest (F1, F2 and F3) and three populations in Second-growth forest (S1, S2 and S3) (Fig. 1) were collected in field during January 2007, 12 pitfall traps per site were installed for 3 days and 3 nights, and separated from each other by approximately 5 m. The sex of each specimen was determined under an optical microscope, based on the presence of antennal careens (Benítez et al., 2010a).

2.2. Shape analyses, samples and measurement error

A total of 477 specimens of *C. chilensis* were used for the morphometric analyses. For each individual we took a picture of the ventral side with an Olympus X-715 digital camera; we then digitized 28 landmarks (LMs, anatomical homologous points) on every picture, by TpsDig 2.10 (Rohlf, 2006) (Fig. 2). All analyses were then run using MorphoJ software version 1.05d (Klingenberg, 2011).

Once obtained the Cartesian $x-y$ coordinates for all landmarks, the shape information was extracted with a full Procrustes fit (Rohlf and Slice, 1990; Dryden and Mardia, 1998), taking into account the object symmetry of the structure. Procrustes superimposition is a procedure that removes the information of rotation, position and orientation and standardizes each specimen to unit centroid size (that is the he square root of the summed squared Euclidean distances from each landmark to the specimen centroid, and provides an estimation of the size of the studied structure (Dryden and Mardia, 1998)). Because of the symmetry of the structure, reflection is removed by including the original and mirror image of all configurations in the analysis and simultaneously superimposing all of them (Klingenberg et al., 2002).

We also provided informations on the studied structure symmetry for observing eventual phenomena of directional asymmetry or fluctuating asymmetry, and to better understand the observed differences between the investigated populations. DA occurs whenever one character developed more in one side of the plane or planes of symmetry than in the other (Van Valen, 1962), while FA is defined as those random differences which occur between the left and right sides in symmetrical organisms. Fluctuating asymmetry has been used as an indicator of the level of developmental stability and in defining the influence of both environmental and genetic stress on development (Van Valen, 1962). Measurement error (ME) is of critical importance when analysing FA (e.g. Palmer, 1994). To assess the significance of FA relative to ME, 50 individual beetles were digitized twice. We then applied a conventional analysis of variance (ANOVA) on centroid size for size and a Procrustes ANOVA for shape taking into account the values of MS of the ANOVA.

2.3. Statistical analyses

To examine the amount of symmetric variation and asymmetry we used Procrustes ANOVA as assessed for studies on object symmetry (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002; Klingenberg and Monteiro, 2005). To avoid the assumption of having an equal and independent variation at all points, we performed a MANOVA test for symmetric component and asymmetry. This test is used to compare the individual–reflection interactions to measurement error, the latter estimated from the total variation of the entire landmark configuration (Klingenberg et al., 2002).

In addiction, the shape variation in the entire data set were assessed using principal component analysis (PCA), based on the covariance matrix of symmetric and asymmetry components of shape variation. The first one is the average of left and right sides and represents the shape variation component, whereas the